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William L. Baker

Thomas T. Veblen

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## SPRUCE BEETLES AND FIRES IN THE NINETEENTH-CENTURY SUBALPINE FORESTS OF WESTERN COLORADO, U.S.A.

WILLIAM L. BAKER\*

*Department of Geography, University of Wisconsin  
Madison, Wisconsin 53706, U.S.A.*

THOMAS T. VEBLEN

*Department of Geography, University of Colorado  
Boulder, Colorado 80309, U.S.A.*

### ABSTRACT

We analyzed 17 photographs, taken between 1873 and 1915, that illustrate widespread mortality in subalpine forests of western Colorado. Eight of these photographs, reproduced here, contain three general patterns of mortality, interpreted to result from spruce beetle (*Dendroctonus rufipennis*) attacks, fires, and wind. Tree-ring chronologies at four of the sites corroborated the role of spruce beetle in killing the trees visible in the photographs. The photographs and tree-ring dates suggest that the spruce beetle outbreak occurred between the 1850s and the 1880s, and affected forests from central New Mexico to north-central Colorado. Spruce beetle outbreaks are a significant type of natural disturbance in these forests. The relative contribution of beetles and fires to subalpine forest structure is in need of further research. The sequence and spatial configuration of disturbances by spruce beetles, fire, and wind varies, and can be spatially heterogeneous, even on small land areas. In such areas, forest responses to uniformly applied disturbance controls (e.g., fire suppression) will be spatially heterogeneous, not affecting all parts of the landscape uniformly.

### INTRODUCTION

Subalpine forests in the southern Rocky Mountains are periodically disturbed by fires, insect attacks, wind, and other agents. Fire is considered to have been the primary presettlement disturbance agent in these forests (Clements, 1910; Arno, 1980; Gruell, 1980a, 1980b, 1983; Peet, 1981, 1988). The intentional suppression of fires since the early 1900s is thought to have encouraged tree density to increase inside forests and trees to invade meadows and shrublands, and to have caused other changes in vegetation (Gruell, 1980a, 1980b, 1983).

In contrast to the research attention devoted to fire his-

tory and postfire stand development in the southern Rockies, the role and history of insect attacks have received scant attention. The most complete information on the pre-20th-century occurrence of insect outbreaks is for *Choristoneura occidentalis* (western spruce budworm), which attacks *Pseudotsuga menziesii* (Douglas-fir), and in some areas *Abies concolor* (white fir), in relatively low elevation forests of the southern Rockies. Major 18th- and 19th-century outbreaks of western spruce budworm in the southern Rockies have been documented using dendrochronology (Swetnam, 1987).

Evidence of past insect outbreaks in subalpine forests is much less complete. The subalpine forests of the southern Rockies are dominated mainly by *Abies lasiocarpa*

\*Present address: Department of Geography, University of Kansas, Lawrence, Kansas 66045, U.S.A.

TABLE 1  
Major spruce beetle outbreaks in the southern Rocky Mountains, based on historical accounts

Event	Dates	Location	Source(s)
1.	1850s–1880s	Pike National Forest, Colorado White River Plateau and Grand Mesa, Colorado	Hopkins (1909) Sudworth (1900); Schmid and Frye (1977)
2.	1892–1904	White Mountains, New Mexico	Schmid and Hinds (1974)
3.	1916–1929	White Mountains, New Mexico Aquarius Plateau, Utah	Hopkins (1909) Schmid and Frye (1977); Schmid and Hinds (1974)
4.	1939–1951	White River Plateau, Arapaho National Forest, Grand Mesa National Forest, Routt National Forest, San Juan National Forest, Uncompahgre National Forest, Colorado	Schmid and Frye (1977); Schmid and Hinds (1974); Miller (1970)
5.	1968–1971	White Mountains, Arizona	Schmid and Frye (1977)
6.	1970s	Wolf Creek Pass, Colorado; Encampment, Wyoming	Schmid and Frye (1977)

(subalpine fir), *Picea engelmannii* (Engelmann spruce), *Pinus contorta* (lodgepole pine), and *Populus tremuloides* (quaking aspen). The last two species are often successional to the first two (Peet, 1981; Veblen, 1986). Insects that may attack and kill the dominant subalpine forest trees include *Dendroctonus rufipennis* (spruce beetle), *D. murrayanae* (lodgepole pine beetle), *Ips* spp. (ips), *Scolytus ventralis* (fir engraver), occasionally spruce budworm, and a few others (Furniss and Carolin, 1977; Alexander, 1987). The subalpine forest insect most likely to have large-scale outbreaks is the spruce beetle; it is also the most damaging subalpine forest insect in the study area (Alexander, 1987). Historical records suggest that there have been approximately six major outbreaks of

spruce beetle that have caused large-scale forest mortality in the southern Rocky Mountains since the middle 1800s (Table 1). It is unclear, however, from Hopkins's (1909) observations whether the 1892–1904 outbreak in the White Mountains of New Mexico is distinct from the mid-1800s outbreak in the same area.

The purpose of this paper is to expand documentation of a spruce beetle attack in western Colorado subalpine forests in the last half of the 19th century, using photographic and dendroecological evidence, and to add to the evidence (Hopkins, 1909) that, while fire is undeniably an important disturbance agent, spruce beetle outbreaks also play an important role in influencing the structure of this region's subalpine forests.

## METHODS

### PHOTOGRAPHS

Repeat photography has been widely utilized as a means to analyze landscape change (Rogers et al., 1984). We located 17 early photographs (Appendix; Figure 1) of subalpine forests showing significant amounts of standing-dead or fallen trees. Eight of these early photographs are reproduced here to illustrate the general condition of these forests between A.D. 1873 and 1915. Contemporary rephotographs are reproduced for four of the sites of the early photographs, to illustrate the pattern of recovery from 19th-century disturbances.

It is important to distinguish between burned and beetle-disturbed forests in the early photographs. We hypothesized that if the mortality evident in the photographs is the result of an insect outbreak, then it probably is a spruce beetle outbreak, as this has been the only major historically recorded insect prone to outbreaks in these forests (Schmid and Frye, 1977). Beetle-disturbed forests are visually distinctive. Spruce beetle may kill up to 99% of the trees that are greater than ca. 20 cm in diameter at breast height (dbh) in a stand, but do not attack *Abies lasiocarpa* of all sizes or most small (< ca.

10 cm dbh) *Picea engelmannii* (Schmid and Frye, 1977). Photographs of forests known to have been killed by spruce beetle during the 20th century (Mielke, 1950; Schmid and Hinds, 1974; Schmid and Frye, 1977) illustrate the following two patterns. Depending on forest composition and the intensity of the outbreak, the result is either (1) a fine-grained "salt-and-pepper" pattern, with alternating live and dead canopy trees, or (2) a forest with dead overstory trees and live subcanopy trees, saplings, and seedlings (Hopkins, 1909; Mielke, 1950; Hinds et al., 1965; Miller, 1970; Schmid and Hinds, 1974; Schmid and Frye, 1977).

Fire behavior in the region's subalpine forests and the appearance of burned subalpine forests have seldom been reported, but fires appear to burn primarily in three ways. First are major stand-destructive crown fires, the most common type of subalpine fire in the Rocky Mountains (Arno, 1980; Heinzelman, 1985). These fires usually kill overstory trees as well as saplings and seedlings:

The fire was less intense in the spruce-fir forest. Although all the trees were killed, branches remained on the trees, and in many locations, a layer of charred duff was present on the surface. (Striffler and Mogren, 1971: 26)

Second are patchy fires, that burn as surface fires for a short distance, then burn the overstory trees for a short distance:

As the fire burns downslope or across slopes, ridges, or small drainages, the topography provides optimal topographic conditions for crowning. The fire then makes a brief run upslope until fuels or topography change. A small open area, denuded

of trees, results. As the fire continues, numerous open areas create a mosaic pattern on the landscape; a pattern that differs from that created by larger stand replacement fires. (Keown, 1985: 244-245)

Such fires produce a coarse-grained mosaic, with patches of dead trees or open areas alternating with patches of surviving trees. Third are surface fires, which are rare.

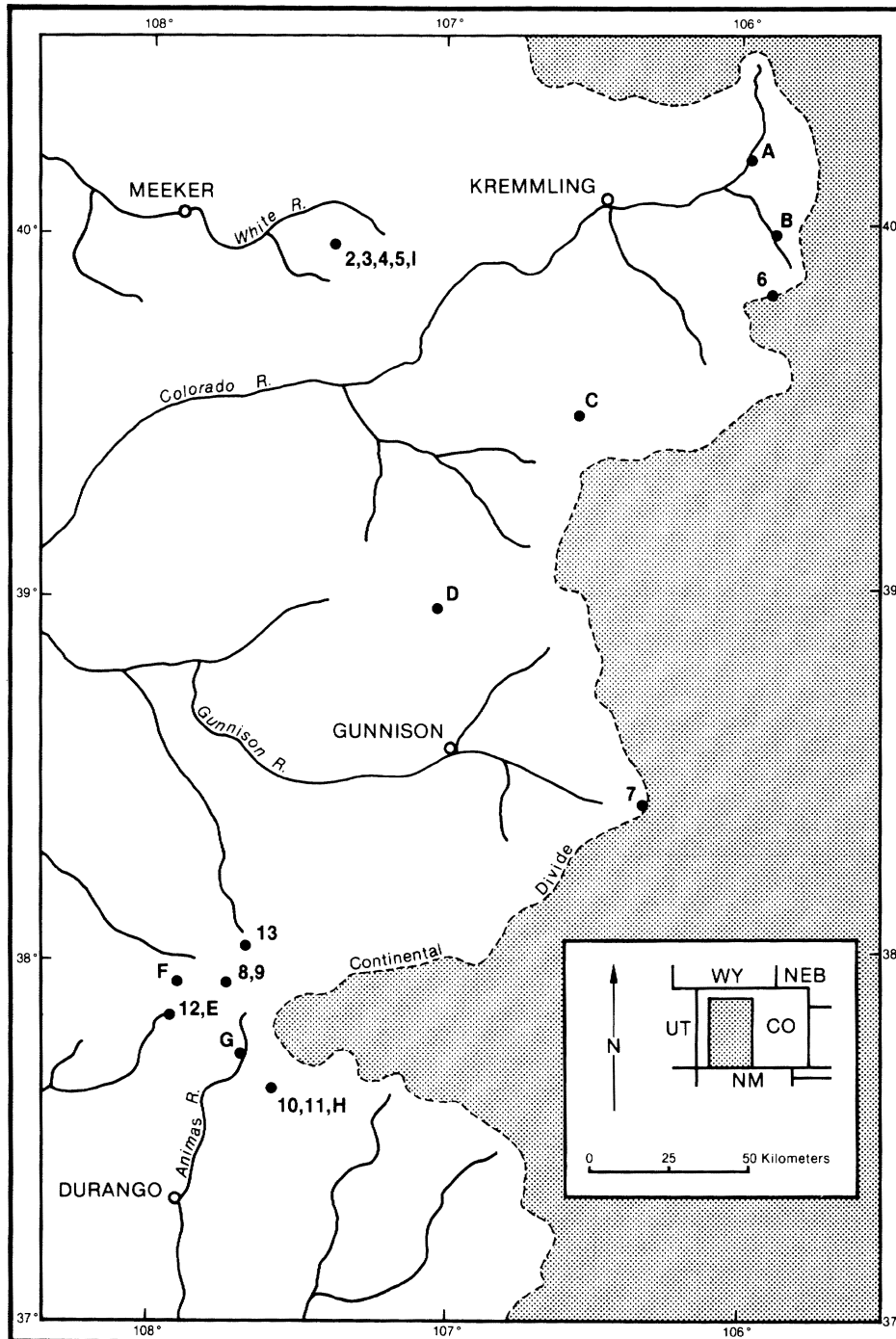


FIGURE 1. Map of the study area. Numbers represent locations for the corresponding figures in this paper. Letters are locations for photographs not reproduced here, but listed in Appendix.

These fires usually do not kill overstory trees, but can occasionally produce localized individual tree mortality or a patchy structure:

Its general behavior was a steady and thorough consumption of the moderately heavy ground fuels, with intermittent spotting and ignition of the crowns. Only in areas of exceptionally heavy fuels, where the heat of the fire generated substantial convection currents, did a crown fire develop. The crown fire died down in lighter ground fuels. (Loope and Gruell, 1973: 430–431)

We could find no evidence, from published fire behavior observations, that fires in these forests can produce the extensive tree-to-tree salt-and-pepper pattern that results from spruce beetle attacks. Moreover, fires do not kill the canopy trees while leaving the subcanopy trees, seedlings, and saplings alive, as spruce beetles usually do. However, if conifers reinvade a forest destroyed by a stand-destructive fire, then a few decades after a fire the forest could conceivably contain standing-dead trees with a live understory of reinvading trees.

These observations suggest that mortality from spruce beetle attacks and fires can, in many instances, be distinguished in old photographs. We suggest that (1) rather solid and continuous areas of fine-grained salt-and-pepper mortality are the result of spruce beetle attacks, not fires, (2) continuous areas of standing-dead trees with no live understory trees, or a coarse-grained mosaic of live and dead patches are, in contrast, probably the result of fires, and (3) continuous areas of standing-dead trees with live understory trees clearly can result from spruce beetle, but could also result, in some cases, from fire.

Dead stems from spruce beetle attacks and fires may remain standing for decades, but their abundance and condition in old photographs provide only a crude means to estimate the time of the mortality. In Utah, 84% of

dead trees were still standing, with branches and twigs largely retained, about 25 yr after death (Mielke, 1950). Mielke also noted that fire-killed spruce in Colorado may remain standing for 50 or 60 yr, and that nearly 70 yr after a spruce beetle outbreak a few of the dead spruce were still standing. Hinds et al. (1965), however, found that about 70% of the dead trees were still standing 20 yr after the White River Plateau beetle attack of 1939–1951 (Table 1). Standing-dead trees from that outbreak are still conspicuous today throughout the White River Plateau.

#### DENDROECOLOGY

Patterns of tree-ring growth were investigated in a stand known to have burned (Figures 2 and 3) and a stand known to have suffered massive beetle-caused mortality in the 1940s (Figures 4 and 5). The two stands were near each other at the White River study site (Figure 1). All live trees >4 cm dbh were cored at ca. 40 cm above ground in five 5 m × 10 m plots (burned stand) and five 10 m × 10 m plots (beetle-disturbed stand) placed in a stratified-random manner in a central part of each stand. Cores were sanded, and ring-widths and ages were determined using a stereomicroscope and an incremental-measuring machine. Ring-widths were measured for four of the oldest 10 trees of each species in each stand. The patterns of ring widths from the stands with known disturbance histories were used as the basis for interpreting tree-ring chronologies from stands of unknown disturbance history.

At three other photographic sites, cores were removed from 3 to 6 of the largest trees currently present in locations where mortality was evident in the early photograph (Figures 6, 7, and 8—at points labelled S). The areas of mortality evident in the photos were searched for evidence of past fires (charcoal and fire-scarred trees). Ring-widths were measured on each core as described above.

## RESULTS AND DISCUSSION

#### RECOVERY PATTERNS IN REPHOTOGRAPHS

Forests at some of the sites that contained many standing-dead trees in the late 19th and early 20th centuries were dominated by live, apparently healthy trees by the 1980s (compare Figures 2 and 3, 8 and 9, 10 and 11). At the other early photograph sites (Figures 6, 7, 12, and 13), similar recovery is apparent in rephotographs (not reproduced here). At one early photograph site, standing-dead trees are evident in both the early 1900s and in the 1980s (compare Figures 4 and 5). This latter site is the site known to have been disturbed by beetles in the 1940s. These and other rephotographs (Baker, 1987) suggest that the mid- to late-19th-century forests of western Colorado were extensively disturbed in comparison with contemporary forests.

#### MORTALITY PATTERNS IN PHOTOGRAPHS

There are four patterns of tree mortality apparent in the photographs. First, the fine-grained salt-and-pepper

pattern, suggesting spruce beetle attack, is apparent in several photos (Figures 4, 6, 8, 10, and 12). Second, a pattern with patches of standing-dead trees, lacking understory survivor trees (Figures 2, 6, 8, 10, and 13) and a pattern with large patches of open ground with scattered standing-dead and fallen trees and no live understory trees (Figures 6, 10, and 13) suggest fires, probably more intense in this case. Third is a pattern with standing-dead canopy trees and live intermediate-sized and small understory trees (Figure 7). This mortality pattern is identical to that in some stands known to have been killed by spruce beetle (Mielke, 1950: Fig. 1B), but could conceivably also result from reinvansion following fire. The last pattern is one with large patches of downed trees, present in only one area (Figure 8—point labelled C), which may have followed mortality from a fire or may have resulted directly from blowdown.

Many of the trees in the salt-and-pepper areas at the time of the photographs (1873–1915) appear to have been



FIGURE 2. View west of Lower Marvin Lake (White River Plateau) at 2830 m (9350 feet) elevation. Point S is the tree-ring sampling site. The forests across the lake contain standing-dead trees killed by fire. (G. B. Sudworth, 1898. Meeker Museum photograph.)



FIGURE 3. Same location as Figure 2. (T. T. Veblen, 1988.)



FIGURE 4. View east of Upper Marvine Lake (White River Plateau). Taken from ca. 2830 m (9350 feet) elevation. Point S is the tree-ring sampling site. The forests near and to the left of S illustrate the salt-and-pepper mortality due to spruce beetle. (W. I. Hutchinson, ca. 1915. Denver Public Library photograph No. 4606.)



FIGURE 5. Same location as Figure 4. (T. T. Veblen, 1988.)





FIGURE 6. Berthoud Pass at 3620 m (11,880 feet) elevation, looking southwest from a ridge approximately 0.3 mi northwest of the pass. Labelled points are: S=the tree-ring sampling site, A=salt-and-pepper mortality due to spruce beetle, B=forest consumed by intense fire. (U.S. Geological Survey photograph No. 1338, W. H. Jackson, 1873.)



FIGURE 7. Marshall Pass at 3353 m (11,000 feet) creek elevation, looking east and downstream from the Continental Divide at Marshall Pass. Point S is the tree-ring sampling site. Extensive mortality is from a spruce beetle outbreak. (Courtesy Colorado Historical Society, photograph No. J-2708, W. H. Jackson, 1886.)



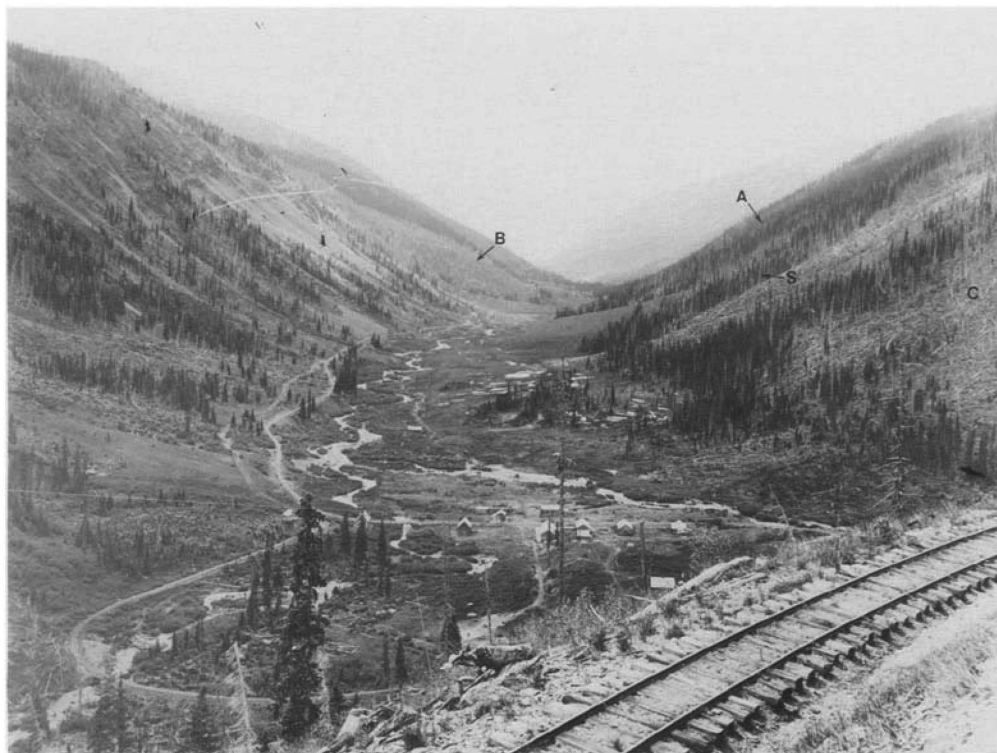


FIGURE 8. Mineral Creek at 3085 m (10,120 feet) creek elevation, looking downstream from about 3 km southwest of Red Mountain Pass, about 10 km northwest of Silverton. Labelled points are: A = salt-and-pepper mortality due to spruce beetle, B = complete mortality due to fire, C = blowdown, S = tree-ring sampling site. (Courtesy Colorado Historical Society, photograph No. J-13830, W. H. Jackson, ca. 1888-1889.)

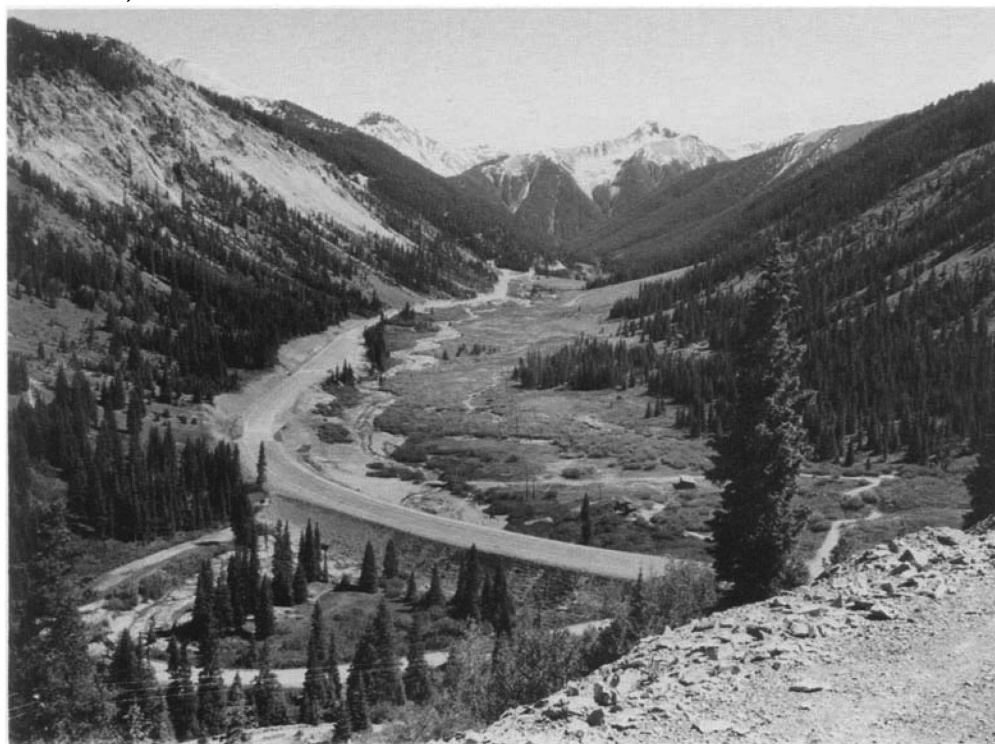


FIGURE 9. Same location as Figure 8. (W. Baker, 1985.)



FIGURE 10. Vallecito Creek at 2780 m (9120 feet) creek elevation, looking upstream from a point about 1 km south of the mouth of Johnson Creek, about 45 km northeast of Durango. Labelled points are: A = salt-and-pepper mortality due to spruce beetle, B = standing-dead trees killed by fire, C = scattered standing-dead trees killed by more intense fire. (U.S. Geological Survey, photograph No. 527, W. Cross, 1901.)



FIGURE 11. Same location as Figure 10. (W. Baker, 1985.)



FIGURE 12. Lizard Head Creek at 3057 m (10,030 feet) creek elevation, near Lizard Head Pass, looking upstream from a point about 3 km southwest of the pass. Forests contain the salt-and-pepper mortality pattern typical of spruce beetle disturbance. (Courtesy Colorado Historical Society, photograph No. J-1637, W. H. Jackson, 1893.)



FIGURE 13. Ironton Park, about 8 km south of Ouray at 2941 m (9650 feet) elevation, looking upstream from the western margin of the park. Labelled points are: A = standing-dead trees killed by fire, B = scattered standing-dead trees killed by more intense fires. (Courtesy Colorado Historical Society, photograph No. J-32578, W. H. Jackson, 1881-1889.)

in a similar state of decay, with numerous side-branches and twigs remaining on the dead stems (Figures 7, 8, 10, and 12). On Marshall Pass (Figure 7), however, dead trees had fewer side-branches, suggesting a slightly more advanced state of decay. The other photographs are not sufficiently clear to allow evaluation of decay state. The high percentage of standing-dead trees, with side-branches and twigs still present, suggests that the mortality continued until perhaps 20 to 30 yr prior to the photographs, or roughly until about 1865–1880. The dendroecological analysis provides further evidence of the timing of the outbreak.

#### DENDROECOLOGY

The patterns of tree growth reflected in the tree-ring chronologies (Figure 14) are different in the postfire stand (Figure 3) and the stand disturbed by the 1940s beetle outbreak at the White River site (Figure 5). In the postfire stand, both subalpine fir and Engelmann spruce attained their maximum growth rates during the first 20 to 40 yr and declined as they aged. In contrast, subalpine fir and Engelmann spruce in the beetle-disturbed stand had growth patterns typical of trees which were long suppressed in the understory and reached the canopy following a major disturbance. The historically documented spruce beetle outbreak of 1939–1951 (Hinds et al., 1965) is reflected by dramatic and sustained releases of all trees beginning in the late 1940s to early 1950s. Most trees also show a period of accelerated growth during the 1970s and 1980s. Given the tendency for spruce to remain standing for many decades after death, this period of secondary release may be the result of more recent blowdown of trees killed in the 1940s.

Many trees at the White River site also show significant releases in the late 19th and early 20th centuries (Figure 14), which may be related to the extensive canopy tree mortality described by Sudworth (1900) and attributed to spruce beetles by Hopkins (1909). Therefore, just as in the case of the 1940s outbreak, more than 40 yr after the initiation of canopy mortality in the 1870s (as estimated by Sudworth, 1900), release was still occurring. The relatively weak releases associated with this earlier outbreak in comparison with the more dramatic growth accelerations following the 1940s outbreak are explained by two considerations. First, apparently the earlier outbreak was not as intense as the 1940s outbreak; Sudworth (1900) describes only 10 to 25% mortality, and the historical photographs also suggest the earlier outbreak was less intense (compare Figures 4 and 5). Second, many of the spruce which were more dramatically released by the 19th-century outbreak would have attained sufficient size so that they were killed in the 1940s outbreak.

At the Berthoud Pass site, where a salt-and-pepper mortality pattern suggesting spruce beetles is apparent in 1873 (Figure 6) tree-ring widths have a complex pattern (Figure 15a–e). In one tree (Figure 15b) sustained slow growth is followed by a release, in 1850, and gradually increasing growth after 1850, reflecting the trends observed at the known spruce beetle site (Figure 14). In

three other trees (Figure 15a, c, and e) there is also a release in 1850 or 1851, and while prior growth was declining, it was not the sustained slow growth expected in a suppressed understory tree. These three trees were approximately 280, 300, and 250 yr old, respectively, and likely were canopy dominants that survived the beetle outbreak. A last tree (Figure 15d) had a dramatic growth decline in 1846–1847 and sustained slow growth until 1864. Diverse responses such as these are to be expected where canopy mortality is patchy and trees die over several years. In such stands the spatial pattern of dead trees determines whether an individual tree will show a release, how pronounced the release will be, and when it will occur. There were no fire scars on any trees in this stand and no charred wood on the ground. The state of the forest in 1873 (Figure 6) is consistent with a spruce beetle outbreak in the late 1840s.

At Marshall Pass, where a clear pattern of nearly complete overstory mortality and understory survival is apparent in 1886 (Figure 7), tree-ring widths on three trees all reflect a release in 1859–1860 (Figure 15f–h). Two of the trees (Figure 15f and g) became established in the early 1800s and grew as suppressed understory individuals until canopy mortality in 1859–1860. The other tree (Figure 15h) probably became established in the 1840s and only grew as a suppressed individual for a few years prior to release in 1859–1860. These are the only old trees that could still be located in the stand, as most of the old trees had been removed by recent selective logging. There was substantial evidence (charred downed wood and scarred trees) of a fire that burned at least several decades in the past. It is possible that the fire occurred around 1900, when two of the trees had a second release (Figure 15f and g). It is not likely that a fire caused the release in 1859–1860, as understory trees could not have survived a fire as abundantly as they did (Figure 7). The live trees apparent in 1886 (Figure 7) are too large to have originated following a fire in 1859 or 1860. Thus, the interpretation is that the pattern in Figure 7 resulted from a locally intense spruce beetle outbreak about 1859–1860.

At the Mineral Creek site, where in ca. 1888–1889 the salt-and-pepper mortality pattern is apparent (Figure 8, point labeled S), tree-ring growth patterns are again complex (Figure 15i–n). Three trees had a release in 1884–1886 following a period of slower growth (Figure 15i, j, and l). These three trees had originated between 1820 and 1850, and probably were growing in the understory and were released by canopy mortality in 1884–1886. This pattern of response is similar to that in the known beetle-disturbed stand (Figure 14). Another tree (Figure 15k), which originated in the mid-1700s, had reached peak growth in the 1830s and declined subsequently. This tree was probably a canopy dominant in the 1880s, and it experienced accelerated growth beginning in the late 1880s, probably following the death of its neighbors. Two other trees (Figure 15m and n) did not respond in the 1880s, but had a simultaneous response in 1911. These trees were within a few meters of each other in the stand. Their response to the 1880s mortality may have been delayed until

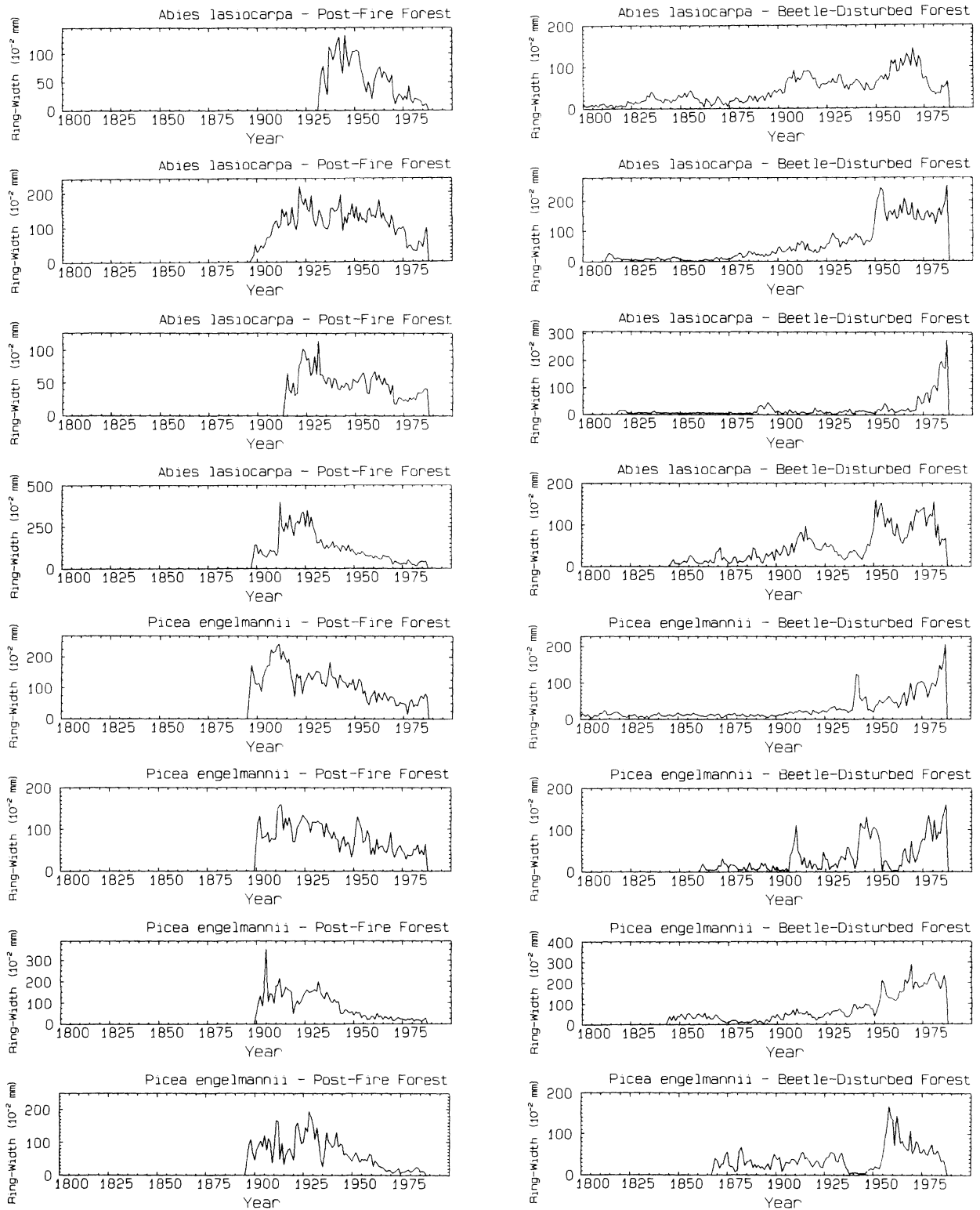


FIGURE 14. Tree-ring widths (mm) versus time (yr) for four trees of *Abies lasiocarpa* (ABLA) and four trees of *Picea engelmannii* (PIEN) in a burned stand (see Figure 2) and a beetle-disturbed stand (see Figure 4) at the White River site (Figure 1).

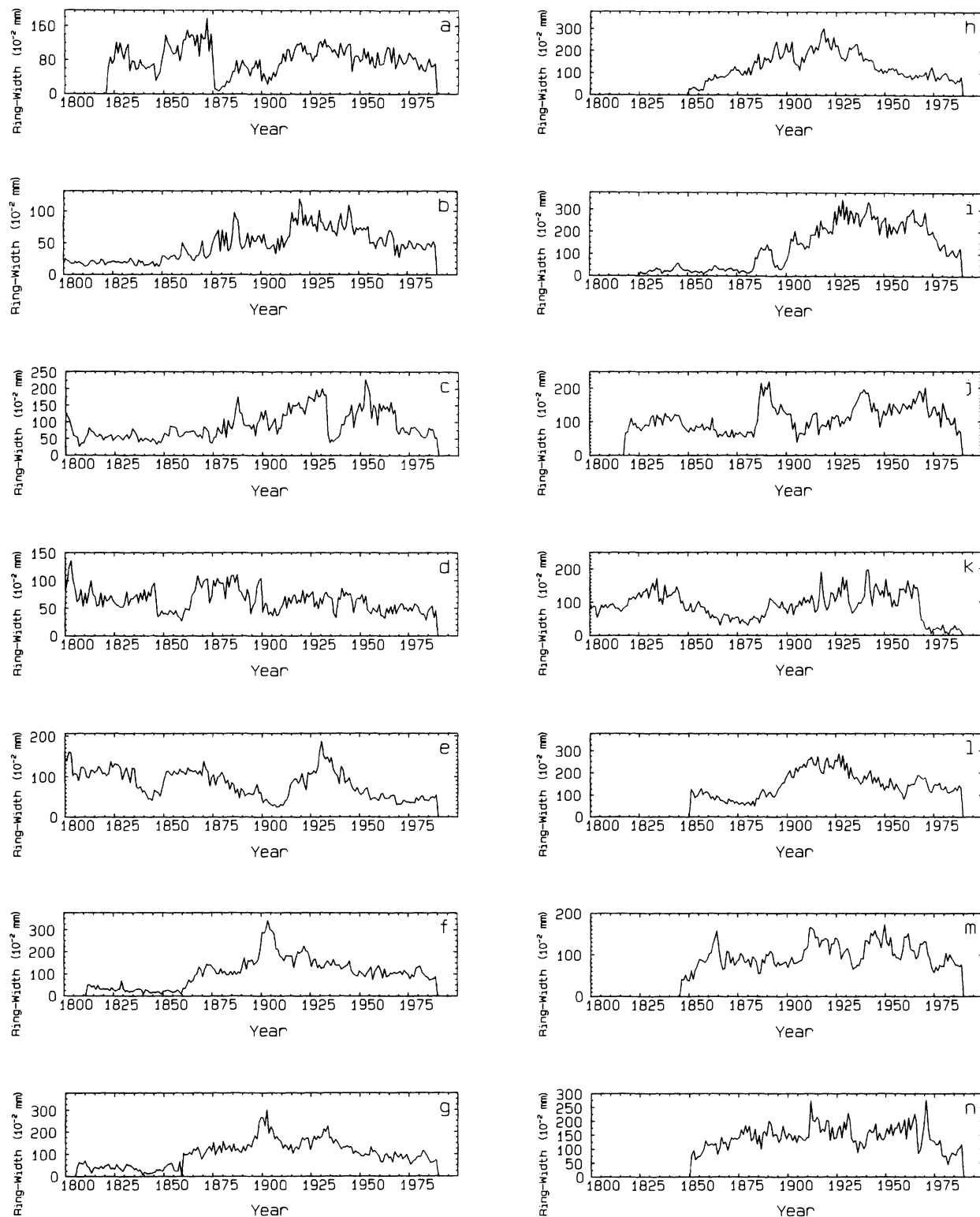


FIGURE 15. Tree-ring widths (standardized) versus time (yr) at Berthoud Pass (a-e; see Figure 6), Marshall Pass (f-h; see Figure 7), and Mineral Creek (i-n; see Figure 8). All tree-rings are from *Picea engelmannii*. For trees that originated prior to A.D. 1800, only the growth patterns since 1800 are illustrated.



a mutual neighbor fell. There was no evidence of recent past fire within the stand. The ca. 1888–1889 photograph (Figure 8) shows clearly that many trees had died by the late 1880s.

#### DISTURBANCES, DISTURBANCE CONTROL, AND LANDSCAPE STRUCTURE

The presence of several mortality patterns at a single photographic site suggests a complex interaction or sequence of disturbance agents. In Figures 6, 8, and 10, for example, a likely sequence is that spruce beetle initially selectively killed trees or patches of trees, producing a salt-and-pepper mortality pattern over much of the landscape. Fires subsequently burned part, but not all, of the beetle-disturbed forests, producing large patches of standing-dead trees and open ground. Winds may subsequently have blown down standing-dead trees in some areas. The result is a complex mosaic of patches with different degrees and sequences of disturbance, even on a small area. In other settings (Figures 4, 12) only the salt-and-pepper beetle-disturbed forests are apparent, although the extent of mortality varies, and there is no clear evidence of fires or blowdown since the beetle disturbance. All of the nine other early photographs that are not reproduced here contain areas of salt-and-pepper mortality, many contain evidence of fires, and there are some areas of blowdown. Overall, these photographs suggest a relatively pervasive spruce beetle attack, varying spatially in intensity, accompanied in some, but not all, cases by fires and blowdowns.

An important ramification of spatially heterogeneous disturbance interactions is that forest responses to uniformly applied disturbance controls (e.g., fire suppression) must also be spatially heterogeneous. Tree density appears to have increased, in the 20th century, on sites that were disturbed by spruce beetles in the 19th century (e.g., Figures 8–11). This could be due to actual regeneration in canopy gaps left by fallen beetle-killed trees, or it could be that as surviving trees grew up the forest simply appears to have increased in density. In either case, density of canopy trees may simply be returning to pre-disturbance levels. Such conifer density increases following beetle disturbance are similar to conifer density increases though by some authors (e.g., Gruell, 1980b) to result primarily from fire suppression. The same apparent change (conifer density increase) could represent either recovery from beetle disturbance or fires. Since the increase in density could have occurred without fire suppression, the effect of fire suppression on beetle-disturbed sites must not necessarily be an increase in density. Thus, fire suppression has heterogeneous effects in landscapes with spatially-complex disturbance patterns (e.g., Figures 6, 8, 10). The actual effect depends on the state of each part of the landscape, particularly when each part was last disturbed and by what agent. Spatially-detailed reconstruction of disturbance history is required in order to determine the causes of forest change in landscapes where disturbances interact on small land areas.

#### THE 1850s–1880s SPRUCE BEETLE OUTBREAK

Spruce beetle outbreaks in the last half of the 19th century were geographically widespread. About 400 ha of forest were killed by spruce beetles, sometime in the late 1880s, on the Lincoln National Forest in New Mexico (Hopkins, 1909), about 400 km south of our study area. An outbreak also occurred on Pikes Peak, about 170 km east of Gunnison (Figure 1), in the 1850s (Hopkins, 1909). Sudworth (1900) described extensive mortality among Engelmann spruce (10 to 25% of the stand) on the White River Plateau, which he estimated to date from the 1870s, but which probably began in the 1850s (Veblen et al., unpublished). Photographic sites in Colorado with a salt-and-pepper mortality pattern (Figure 1; Appendix) suggest that the 1850s–1880s spruce beetle outbreak affected subalpine forests throughout much of western Colorado.

The salt-and-pepper mortality pattern is also apparent in the subalpine forests of northwestern Wyoming in late-1800 photographs (Gruell, 1980a: Plates 1a, 3a, 4a, 54a, 80a, 83a, 84a). This mortality is attributed in part to unidentified insects and in part to fires (Gruell, 1980a). If spruce beetles were in part the mortality agent in these Wyoming forests, then the 19th-century spruce beetle outbreak may have been roughly contemporaneous along 1200 km of the Rocky Mountain axis. Other insects, however, including mountain pine beetle (*Dendroctonus ponderosae*) may disturb these northern forests (Gruell, 1980a), and additional research is required in order to determine which insect caused the mortality in this area in the late 19th century.

#### FIRES AND INSECT ATTACKS IN ROCKY MOUNTAIN SUBALPINE FORESTS

The data presented here do not contradict Hopkins's (1909: 127–128) contention that: “there has been a most intimate interrelation of destructive barkbeetles and forest fires in the denudation of the vast areas of once heavily forested lands in the Rocky Mountain region, and that in very many cases the insects have first killed the timber, and the fire has then followed . . . , leaving the charred trunks and logs as apparent proof that the fire alone was responsible.” Widespread fires in the last half of the 19th century, when insect-killed trees were common, and the scarcity of fires in Rocky Mountain subalpine forests since that period (Loope and Gruell, 1973; Jones and DeByle, 1985) might suggest that insect disturbances are precursors of large fires. However, the situation is confounded by the high frequency of human-caused fires during the late 19th-century period of mining and settlement (Veblen and Lorenz, 1986). Thus it is difficult to determine whether spruce beetles did or did not increase the susceptibility of these forests to natural fires.

Nonetheless, the data and analysis presented here suggest that the primacy of fire in these forests needs to be reconsidered. Although not sufficient to clearly rank the relative contributions of fire, spruce beetle outbreaks, and wind in subalpine forests, our data support the view that



in many areas insect outbreaks may have played a role comparable to that of fire. Interaction between these disturbances is apparent and major roles for both spruce beetles and fires are suggested.

#### ACKNOWLEDGMENTS

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#### APPENDIX

##### *Sources and locations of photographs illustrating 19th-century insect attacks in the subalpine forests of the study area*

Figure <sup>a</sup>	Photographer	Photo No.	Source <sup>b</sup>	Photo location	Date
2	Sudworth, G. B.		MM	Marvine Lakes	1898
3	Veblen, T. T.		CU	Marvine Lakes	1988
4.	Hutchinson, W. I.	4606	DPL	Marvine Lakes	ca. 1915
5.	Veblen, T. T.		CU	Marvine Lakes	1988
6	Jackson, W. H.	1338	USGS	T3S R75W S9 SE4	1873
7	Jackson, W. H.	J-2708	CHS	T48N R6E S24 SE4	1886
8	Jackson, W. H.	J-13830	CHS	T42N R8W S23 SW4	1888-9
9	Baker, W. L.		KU	T42N R8W S23 SW4	1985
10	Cross, W.	527	USGS	T39N R6W S4 SE4	1901
11	Baker, W. L.		KU	T39N R6W S4 SE4	1985
12	Jackson, W. H.	J-1637	CHS	T44N R9W S23 SE4	1893
13	Jackson, W. H.	J-32578	CHS	T43N R7W S29 SW4	1881-9
A	Jackson, W. H.	1051	USGS	Grand Lake	1874
B	Lake, H. H.	F-43585	CHS	T1S R75W S5 NW4SW4	ca. 1900
C	Jackson, W. H.	1340	USGS	Holy Cross Mountain	1873
D	Jackson, W. H.	1380	USGS	T12S R86W S34	1873
E	Jackson, W. H.	J-4216	CHS	T41N R10W S26 NW4NE4	1890-1
F	Jackson, W. H.	550	USGS	T41N R9W S8 NW4SW4	1875
G	Jackson, W. H.	J-2887	CHS	T40N R7W S17 SE4	1882
H	Cross, W.	526	USGS	T39N R6W S4 SE4	1882
I	Gale, H. S.	236	USGS	Sleepy Cat Peak	ca. 1915

<sup>a</sup>Photos with letters in this column are not reproduced in this paper, but their locations are mapped on Figure 1.

<sup>b</sup>Sources are CHS=Colorado Historical Society, Denver, Colo.; DPL=Denver Public Library, Western History Collection; USGS=U.S. Geological Survey Photographic Library, Denver, Colo.; KU=University of Kansas, Department of Geography—Baker, personal collection; CU=University of Colorado, Department of Geography—Veblen, personal collection; MM=Meeker Museum, Meeker, Colo.

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